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POPULATION DYNAMICS OF TULE ELK AT POINT REYES NATIONAL SEASHORE, CALIFORNIA

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Abstract: The presence of locally abundant wildlife raises questions among wildlife managers about natural regulation and ecological consequences of over population. The purpose of our study was to establish precise information about population size, structure, and productivity to examine the role of natural regulation in a closed tule elk (*Cervus elaphus nannodes*) population at Point Reyes National Seashore. We estimated an exponential growth rate of 0.19 with an adjusted $R^2 = 0.98$, 20 years after the elk were introduced. We estimated survivorship for adult cows of nearly 0.95. Calf survivorship from birth through the rut ending in October-November was 0.85. Male calves exhibited higher mortality than female calves, while cow mortality we observed was associated with the calving season. We measured a 42% increase in cow calf density form 0.733 ha^{-1} to 1.043 ha^{-1} in 1996 to 1998. We observed a density correlated reduction in the rate of increase and in the cow:calf ratios prior to high precipitation El Niño years, 1993, 1996 and 1997, precipitation > 1023 mm $year^{-1}$. Given the high population growth rate and model evaluation of management scenarios, park managers will need to use a suite of approaches to maintain the elk population at levels at or near the closed range carrying capacity.

INTRODUCTION

Tule elk (*Cervus elaphus nannodes*) are a subspecies of elk isolated from other populations of elk during the Wisconsin glacial period over 70,000 years ago and are endemic to California (Bryant and Maser 1982). Once abundant in the state, tule elk were driven to near extinction by the latter quarter of the 19th century, only 6-10 individuals remained on a private ranch in the San Joaquin Valley (McCullough 1969). Early conservation efforts and reintroduction efforts during the latter half of twentieth century have resulted in a statewide recovery of tule elk populations to an estimated 3,500 animals (Jon Fischer personal communication).

In March of 1978, 10 adult elk (2 males and 8 females) were reintroduced to Point Reyes National Seashore (NS) from the San Luis National Wildlife Refuge (Gogan 1986). The elk were placed on a 1,052-ha enclosed range on the northern tip of Tomales Point (Fig. 1). Prior to the complete removal of beef cattle in 1980, the range was characterized by high stocking rates of cattle and low forage quality (Gogan 1986). During the initial period 1978 to 1980, growth of the elk herd was constrained by trace element deficiency, infection with Johne's disease (*Mycobacterium paratuberculosis*) affecting subadult survival, and low reproductive rates (Gogan 1986). After the removal of cattle in 1980 the population grew at a higher rate (Gogan and Barrett 1987). Early research on vegetation estimated the carrying capacity of the herd between 140 and 350 animals (Gogan 1986). By 1990, the elk herd had reached the lower bounds of that estimate and by 1993 had reached an estimated 214 individuals (W. Shook personal communication, Wahome 1995).

In response to increasing numbers of elk, the National Park Service (NPS) commissioned an advisory panel of 6 scientists to examine available elk data and to recommend actions for NPS management of the tule elk herd (McCullough et al. 1993). McCullough (1992:969) defined carrying capacity (KCC) as the "maximum number of animals of a given population supportable by the resources of a specified area." The panel estimated KCC at 346 elk, assuming density-dependent population regulation (McCullough et al. 1993). In addition the panel recommended (1) permitting the elk population to self-regulate unless a predefined threshold of ecological damage to the range was reached, (2) establishing a pilot study to assess the feasibility of utilizing contraceptives as a means of population control, (3) beginning a program of fecal culture and necropsy to establish the status of Johne's disease and potentially other livestock diseases, (4) expanding the habitat and elk population monitoring program, (5) importing two to three female elk every generation, and (6) re-establishing free-ranging elk on other NPS lands. This study was designed to address part 4 of the research recommendations offered by the scientific panel (McCullough et al. 1993) and to assist in meeting the goals of tule elk management at Point Reyes NS (NPS 1988, 1992). In 1997, park managers decided to conduct contraception trials on a subset of the Tomales Point herd. Thirty cows were captured and inoculated with PZP (Stoops et al. 1999, S. Shideler, personal communication).

Precise measures of population size, structure, and productivity are necessary to develop accurate estimates of population growth. Accurate estimates of population growth and habitat use are critical in defining the bounds of KCC for the Tomales Point elk herd. If density-dependent factors are controlling this population, we would expect the net reproductive rate of the population in a year (λ) to approach unity ($\lambda = 1$) and the intrinsic rate of increase (r) to approach zero (r = 0) as the population approaches KCC for a given resource state. We define population growth as:

$$N_t = rN_{t-1} \text{ where } r = dN/dt \qquad (1)$$

N is the population size and t is time in years. If λ remains above one, the population will overshoot KCC with potentially negative impacts to elk habitat. Refined estimates should indicate whether density related mechanisms are operating as this herd approaches KCC.

In this paper, we examine the population size, structure, and productivity of the Point Reyes NS tule elk herd relative to the question of natural regulation (Houston 1982). We report on age-specific mortality, cow:calf ratios, natality rate, sex ratios, and population density 20 years after initial introduction.

STUDY AREA

Point Reyes NS is a 28,827-ha national park located in west Marin County, California (Fig. 1). The park is located approximately 60 km northwest of San Francisco. The elk are confined to the northern tip of Tomales Point, a northwest-trending peninsula bounded on the east by Tomales Bay, on the west by the Pacific Ocean, and a 3-m tall fence that separates the 1,052-ha range from the active dairy ranch to the south.

The elk range can be classified into four habitat types: open grassland (supporting both annual and perennial grasses and forbs), lupine (*Lupinus arboreus*) grassland, coyotebush (*Baccharis pilularis*) grassland, and dense scrub (Fig 1). Three federally listed rare plant species occur locally: Point Reyes blennosperma (*Blennosperma nanum* var. *robustum*), North Coast bird's beak (*Cordylanthus maritimus ssp. palustris*), and San Francisco owl's clover (*Tryphysaria floribundus*). In addition the Myrtle's silverspot butterfly (*Speyeria zerene myrtheae*), a federally listed endangered species, occurs within the elk range. Three larger predators have been observed on the elk range, coyote (*Canus latrans*), bobcat (*Felis rufus*), and mountain lion (*Felis concolor*).

The climate of the elk range is Mediterranean with most rainfall occurring between November and March. Annual precipitation totals fluctuate considerably between wet and dry years. Between 1978 and 1996, average precipitation 16 km due north of Tomales Point at Bodega Marine Laboratory was 853.3 mm (SE = 75.9, n = 19)(unpublished data, V. Chow personal communication). However, average precipitation for wetter-than-normal El Niño events, 1982-83, and 1995-96 was 1364.4 mm 9 SE = 110, n = 4). The average temperature varies between 7° in the winter and 13° C in the summer.

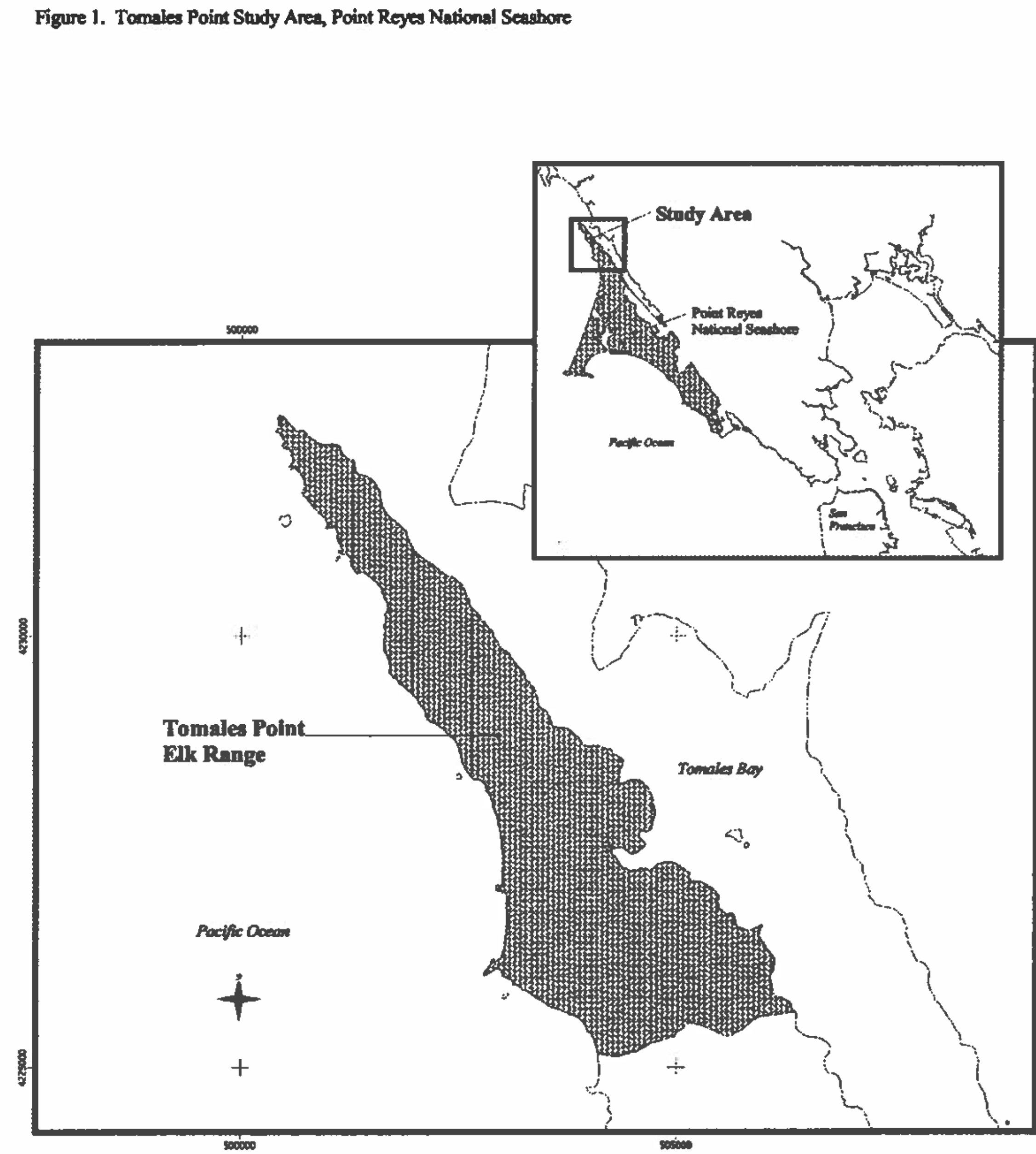

Figure 1. Tule elk (*Cervus elaphus*) range, Tomales Point, Point Reyes National Seashore, California

METHODS

Capture Techniques

Adult female elk were captured in November 1995 and October 1996 with helicopter-deployed ballistic nets (Helicopter Wildlife Management, Salt Lake City, UT). Elk were blindfolded and hobbled upon capture. Processing teams measured total length and girth, monitored vital functions, estimated animal age by examining teeth and body size, and collected blood and fecal samples to determine pregnancy rates and screen for Johne's disease. Blood and fecal samples were transported to Madison WI for Johne's disease testing and to UC Davis for pregnancy testing (Stoops 1999, S. Shideler personal communication). A color-coded radio collar (Telonics, Inc., Mesa, AZ 85204), with mortality sensor and a breakaway device was attached to each cow. The breakaway device had a field life of 7 to 10 years based on studies of elk in Redwood National Park (R. Golightly personal communication). Radio collar transmissions were set for alternate days to extend the expected transmitter life to 7 years from the time of attachment to the elk.

Researchers, on foot or horseback, captured calves in the spring (March through June) of 1996, 1997, and 1998. Cows were approached by horseback and were observed looking in the direction of potential calf bedding areas. Potential calf bedding areas were searched in a back and forth pattern. Once located, bedded calves were approached on foot and captured by hand by placing a blindfold or hat over their eyes. All calves were weighed, measured, and fitted with color-coded ear tags to identify individuals. In 1996, calves were fitted with solar-powered radio ear tags (Advanced Telemetry Systems, Isanti, MN 55040). This practice was discontinued in 1997. In all years, calf mortality was determined by assuming that marked calves not seen for two weeks had died.

Herd Size and Structure

The population was monitored weekly by visual observation from horseback of bothmarked and unmarked individuals. The elk range was searched for groups of elk from highlands until the entire range was explored. In the field, locations for each collared female and tagged calf were marked on USGS 7.5-minute topographic quad sheets and/or field notes. For each relocation point we recorded data about habitat, behavior, and herd composition classes, adult cows, calves, spike bulls, bulls, and prime bulls. Universal Transverse Mercator (UTM) coordinates for relocation points were determined by analysis of the field maps and notes and transferred to computer files using AutoCad Lt (AutoDesk, Inc., San Rafael, Ca 94903) and ArcView 3.1 (Environmental Systems Research Institute, Inc., Redlands, CA 92373).

Each October after the rut, simultaneous aerial and ground counts of the entire herd were conducted to determine the number of cows, calves, spike bulls, and bulls using fixed-wing aircraft censuses, drive counts (McCullough 1997), and herd structure counts. We conducted herd structure counts from horseback over a period of several days. In addition, calf counts were conducted during the summer and fall of each year in order to measure productivity. Natality of each collared cow and marked calf survival were recorded for each year of the study to determine if she had reared a calf to maturity that is until after the rut in October. Production of female offspring was estimated from the annual calf searches. In 1997, we surveyed the entire elk range on horseback weekly for bulls and intermittently in 1998. Location, numbers, and age composition of the groups were recorded.

Estimates of population size from year to year provided a means of calculating of population growth, and formed the basis for demographic projections such as estimating KCC. To estimate r we used the average of *d*N/*dt* for all years. To derive a second estimate of r we used a statistical curve-fitting program, SPSS 8.0 (Norusis 1988a, 1988b). The age and sex structure of the herd was modeled using the original data set for the introduced herd (Gogan 1986) as a baseline. We calculated the number of calves surviving each year (t) by subtracting the previous year total population (N_{t-1}) from the current year total population (N_t). Two then divided the number of calves. To obtain and estimate of sex ration, if there was an odd remainder, we added it to the female calves for that year assuming a slightly higher mortality among male calves. We began the model in 1984 and extrapolated through 1998.

Mortality and Survivorship

In 1996, we conducted systematic mortality searches in three areas of high herd use, grassland and moderate to dense coastal scrub of 38, 35, and 40-ha respectively. We systematically searched each area with 7 people evenly spaced across the width of the search area and walked a zigzag pattern to maximize coverage of the ground. We subsequently discontinued this practice because we recovered few elk remains and the mortality rates within the herd were low. Since most of the range was covered by horseback including heavy brush on a biweekly basis, we substituted opportunistic remains discovery for the systematic ground searches. Records were kept of known instances of mortality from both the instrumented sample and general population. If an individual disappeared between sequential ground counts, we compared the result with mortality records to infer actual mortality rates.

We estimated mortality, conversely survivorship, rates of females from the collared sample by pooling all years and by taking the mean of each year's proportion mortality to derive two linear survival rates. We also estimated a third survivorship curve from cows tagged during the first introductions or as calves born through 1981 and observed in subsequent field surveys.

Density

We used the relocation points to estimate herd range size using the adaptive kernel polygon method, 50% and 90% C.I. using home range software (TELEM 1.0, USDA, Forest Service)(Worton 1989). We used relocation data from the first year to calculated individual home ranges for all instrumented cows. We randomly selected a subset of the individual relocations to establish herd range size and found no difference in herd range size between the random subset of relocation points (n = 20/elk) and all the relocation points. By visual inspection two patterns became clear, individuals clustered in the northern or southern part of the range. We examined individual movements and found virtually no exchange among individuals between north and south in 1995 and 1996. In subsequent years we had 2 individuals switch groups while several more cows made one excursion and returned. We assumed that, although the individuals may move randomly within a herd, the 2 sub-herds were basically geographically stable. We used 4,229,000 UTM North as the cut off line between the 2 sub-herds, which corresponded to the middle of the high plateau between the more varied relief to the north and south. We pooled the relocation records for all individuals in a sub-herd by season to estimate herd range size and calculate high and low habitat use areas. We estimated population density for each year by using the number of animals seen in the sub-herd and calculating mean herd range size at the 90% CI across four biological seasons — calving (April and May), summer (June and July), the rut (August through October), and winter (November through March). In 1997, we surveyed the entire elk range on horseback weekly for bulls. Location, numbers, and age composition of the groups were recorded. We did not record individual bulls but used group and solitary animal locations to establish relocation points. Cow relocation data and bull count data were considered independent and cow and bull range use was mapped separately.

Herd Growth Stabilization Modeling

Greene et al. (1998) developed a breeding system based model, written in BASIC, to model population growth rates under different management scenarios. Assumptions of the model were; (1) equivalence of individuals (all individuals of a given age/sex class were equally likely to reproduce or die), (2) population processes were density-independent (there is no carrying capacity or other source of regulation), (3) population processes do not depend upon population special structure, and (4) reproduction takes place after mortality for ease of computation (C. Greene personal communication). We used our empirically derived population parameters to drive Greene's model to examine the relationship and effectiveness of removal and/or contraception (S. Shideler, personal communication) rates to reduce the net reproductive rate of the Tomales Point herd to zero.

Statistical Analyses

For comparisons we performed Pearson Chi-square (X^2) test of significance ($p< -0.05$) (Lehmann 1975; Norusis 1988a, 1988b).

RESULTS

We captured 20 in November 1995 and 18 adult female elk in October 1996. The day after the first capture one cow died from capture myopathy leaving 19-instrumented cows in 1995. Blood samples from the original 19 cows revealed 16 were pregnant (Stoops et al. 1999). Three cows captured in 1995 died during the 1996 calving season. In 1996, 1997, and 1998, we captured 12, 26, and 28 calves, respectively. Sixteen of the 66 marked calves were born to marked cows over the three-year period. While most calving consistently occurred during April and May, births were documented as early as February and as late as August.

Herd Size and Composition

The total population counts for 1996, 1997, and 1998 were 370, 465, and 549, respectively (Fig. 2). During 1996 and 1997 total counts by horseback, ground, and airplane were within plus or minus fifteen animals (Table 1). The annual rates of population increase (*r*) in our study for 1996 through 1998 were 0.32, 0.26, and 0.19. The 1998 calf count of 87 was lower than the expected 120 calves possibly due to the inoculation of 30 cows contracepted with (PZP) in the fall of 1997 (S. Shideler personal communication). For 1981 through 1997, mean r was 0.22 (SE = 0. 022, n = 17, Min. = 0.08, Max. = 0.41). An exponential model provided the best fit to the observed data (r = 0.1943, $R^2 = 0.984$) for 1981 through 1997. Thirteen of the 16 cows that survived for 3 years had at least 1 calf with an average of 2.076 calves female^{-1} (Fig. 3).

Using linear regression there was no significant reduction in population growth rate with increasing population size through 1997 (Fig. 4A). If we removed the high productivity El Niño years of 1983, 1993, 1996, and 1997, that is precipitation > 1024 mm yr^{-1}, we found a significant negative linear relationship ($p = 0.025$, $R^2 = 0.447$) (Fig. 4B). If the dry year declining rate of growth was constant, the intercept of the abscissa for r = 0 would be about 360 animals by the year 2000. A quadratic model best described the decline in cow:calf ratios with population size between El Niño years ($p = 0.000$, $R^2 = 0.768$, $N = 112.263 - 0.6560x + 0.014x^2$)(Fig 5.). The proportion of calves 100^{-1} cows (Table 2) was positively correlated with precipitation for any given year (t) and the prior year (t – 1) (Fig. 6A, 6B). A multiple regression model for the proportion of calves 100^{-1} cows and the two precipitation parameters was highly significant (Table 3)

Our herd-composition model predicted 9.6% more adult bulls and 7.7% fewer adult cows than observed during herd counts (Table 4). The estimated herd structure for 1997 and 1998 were not significantly different from the observed herd counts using a Chi-square test.

Mortality and Survivorship

During the 1996 systematic mortality searches of 113 ha, we discovered the remains of two cows. We divided the total area of the elk range (1052ha) by area sampled (113ha) and multiplied the number of carcasses (2) discovered to estimate that 18 sets of remains of various age would be found across the range. During our opportunistic recoveries, we collected 15 specimens that is the same order of magnitude we predicted would be found. From the remains of 15 animals we constructed a simple, *a posteriori* life histogram for the herd (Fig. 7).

In 1996, 3 collared cows died during the spring calving season. No evidence of wasting or diarrhea showed in the three. One cow was last seen alive with a prolapsed uterus. We could not determine the cause of death for two; we assumed the third died of complications associated with the prolapsed uterus. During the fall cow capture of 1996, we recovered a fresh bull carcass with a broken jaw.

Two animals were removed from the population in 1997 after they exhibited signs of scouring. One tested positive on fecal culture for Johne's disease while the other did

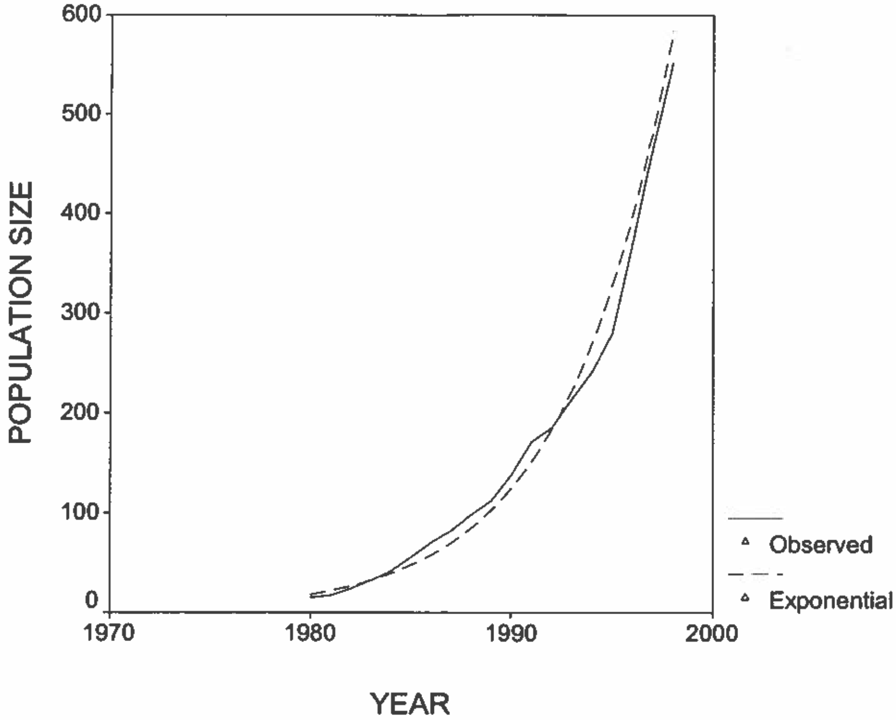

Figure 2. Tule elk (*Cervus elaphus*) population growth, observed versus exponential model, 1978-1997, Point Reyes National Seashore, California.

Table 1. Herd composition counts of Tule elk (*Cervus elaphus*) using aerial counts, drive counts and horseback search counts, Point Reyes National Seashore, California.

Method		Year 1996	1997	1998
Aerial (Fisher)	Total	385		
	Bull/spike/cow/calf	91/4/222/66		
Drive (McCullough)	Total	381	465	
	Bull/spike/cow/calf	72/10/253/46	110/71/240/42	
Horseback	Total	370	465	549
	Bull/spike/cow/calf	90/19[a]/179/80	122/48/218/77	161[b]/45[a]/256/87

[a] Estimated from number of calves born the previous year.
[b] Estimated from spring bull counts.

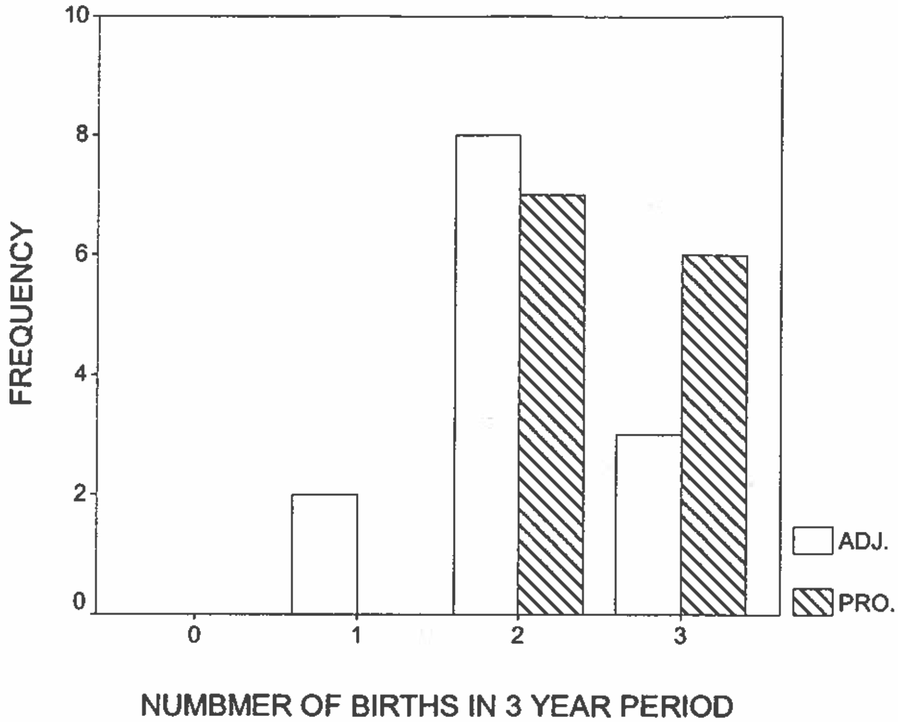

Figure 3. Number of elk calf births to radio collared cows that survived the three years of this study, 1996-1998, Point Reyes National Seashore, California. (ADJ. = values adjusted conservatively based on field observation, PRO. = values projected from field observations)

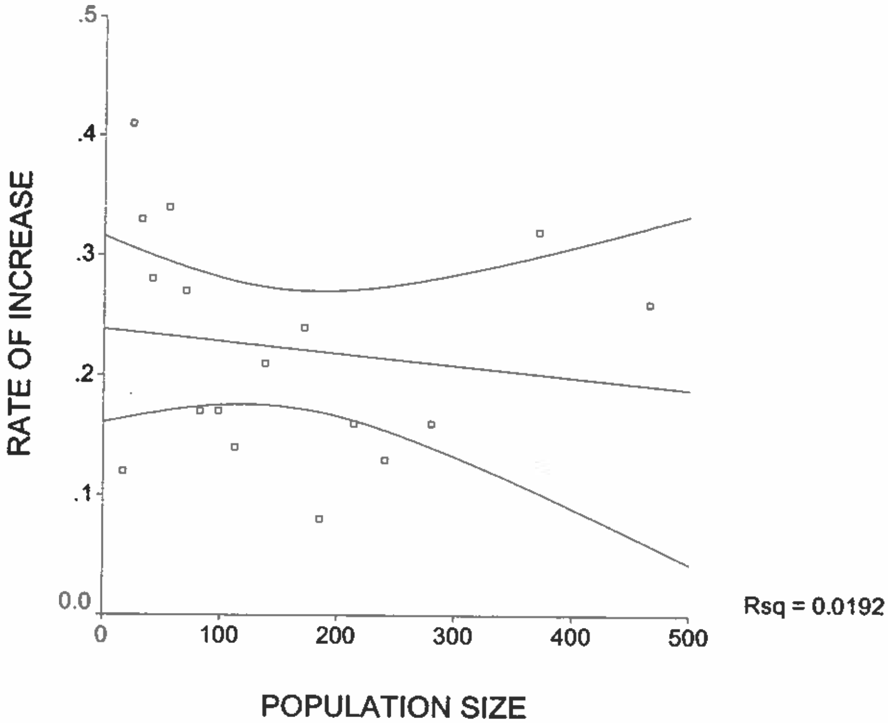

Figure 4A. Tule elk (*Cervus elaphus*) population growth rate versus population size, (A) Including El Niño years, (B) Inter-El Niño years, Pt. Reyes National Seashore, California.

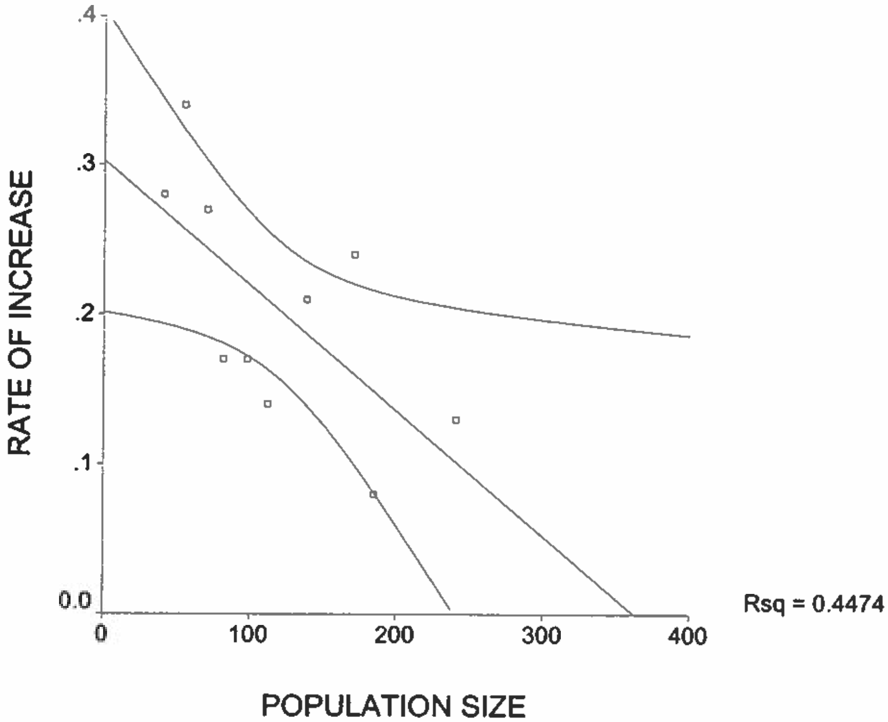

Figure 4B. Tule elk (*Cervus elaphus*) population growth rate versus population size, (A) Including El Niño years, (B) Inter-El Niño years, Pt. Reyes National Seashore, California.

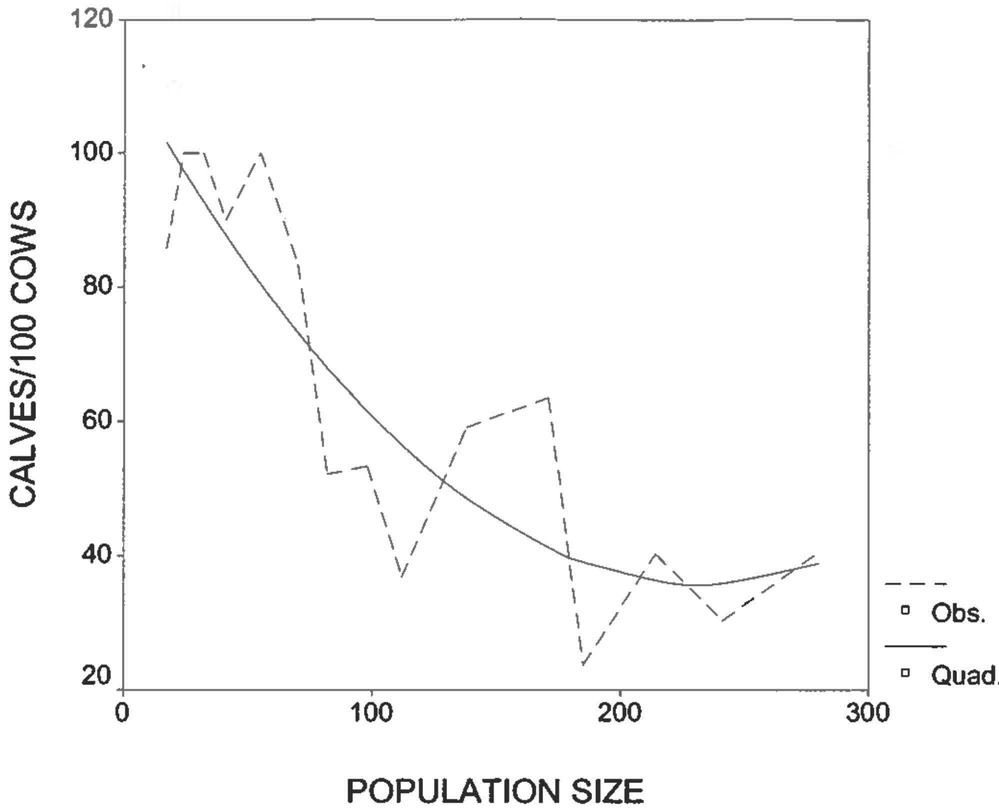

Figure 5. Cow:calf ratio versus population size of tule elk(*Cervus elaphus*) during dry years between El Niño, Pt. Reyes National Seashore, California.

Table 2. Tule elk (*Cervus elaphus*) cow:calf ratios, Point Reyes National Seashore, California.

YEAR	Cow:Calf Ratio 3 Years or Older	Cow:Calf Ratio 2 Years or Older
1980	16.67	12.50
1981	85.71	75.00
1982	100.00	100.00
1983	100.00	80.00
1984	90.00	64.29
1985	100.00	77.78
1986	83.33	65.22
1987	52.17	40.00
1988	53.33	42.11
1989	36.84	31.82
1990	59.09	50.00
1991	63.46	55.93
1992	23.73	19.44
1993	40.28	32.58
1994	30.34	28.13
1995	40.63	35.14
1996	81.08	72.00
1997	76.00	65.52

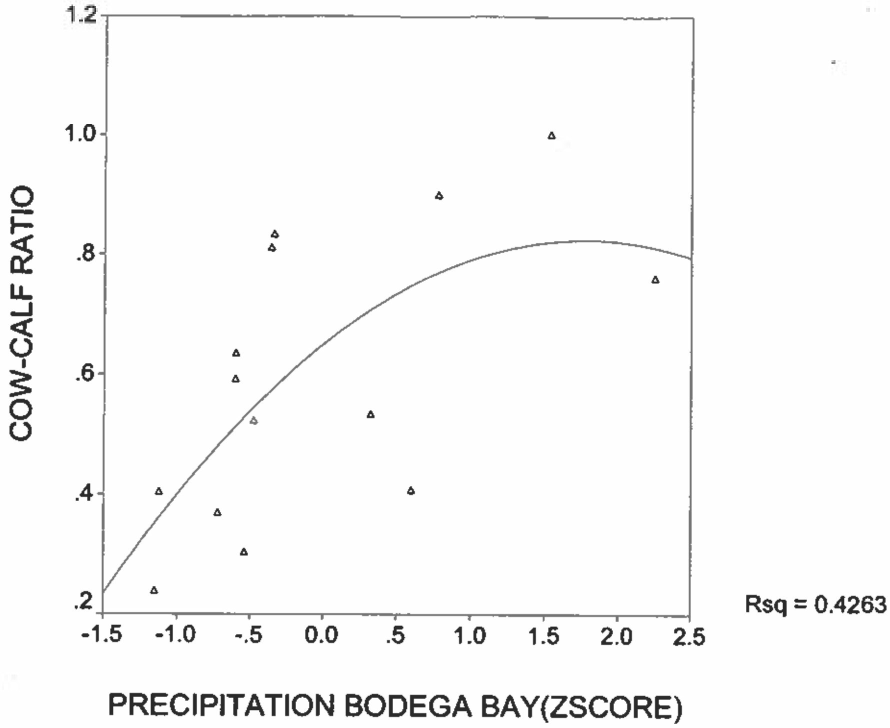

Figure 6A. Tule elk (*Cervus elaphus*) cow:calf ratios, Pt. Reyes National Seashore, California, versus annual precipitation, University of California, Bodega Marine Laboratory, Bodega Bay, California, (A) Current year precipitation, (B) Previous year precipitation.

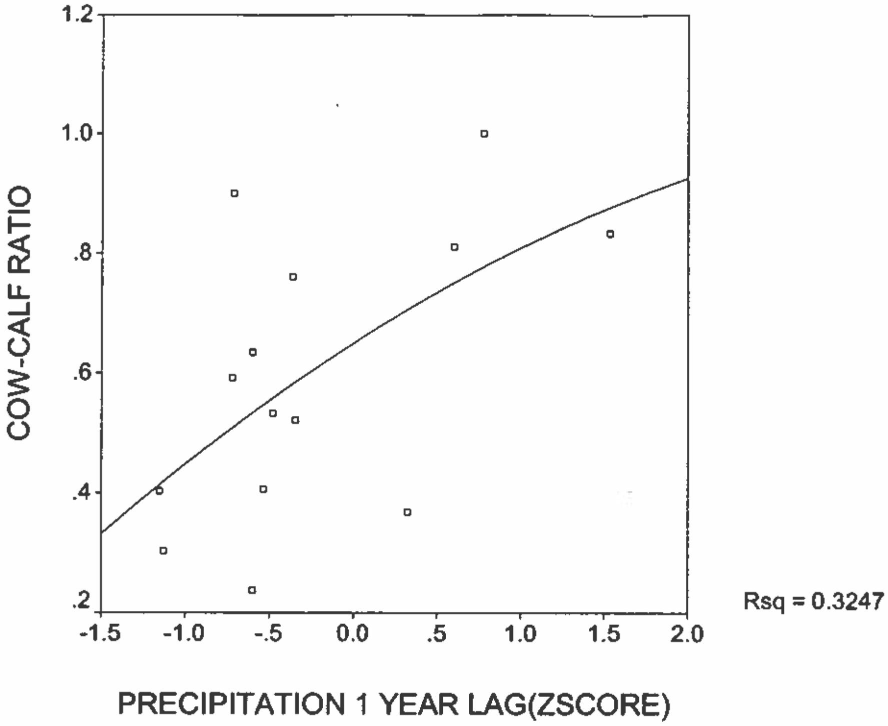

Figure 6B. Tule elk (*Cervus elaphus*) cow:calf ratios, Pt. Reyes National Seashore, California, versus annual precipitation, University of California, Bodega Marine Laboratory, Bodega Bay, California, (A) Current year precipitation, (B) Previous year precipitation.

Table 3. Multiple regression of cow:calf ratio versus precipitation during current year and 1 year time lag from 1984-1997, at Bodega Bay, California.

Model Summary

R	R Square	Adjusted R Square	Std. Error of the Estimate
0.768	0.590	0.516	0.1655

ANOVA

Model	Sum of Squares	df	Mean Square	F	Sig.
Regression	0.434	2	0.217	7.921	0.007
Residual	0.301	11	0.027		
Total	0.735	13			

Coefficients ([a]precipitation)

Model	Unstandardized Coefficients		Standardized Coefficients	T	Sig.
	B	Std. Error	Beta		
(Constant)	0.633	0.047		13.582	0.000
PPT[a] Current	0.125	0.047	0.527	2.684	0.021
PPT + 1 year	0.146	0.061	0.472	2.407	0.035

Table 4. Tule elk (*Cervus elaphus*) herd composition, Point Reyes National Seashore, California.

			Expected[a]		Observed[b,c]		
YEAR	N	CALF	BULL	COW	BULL	COW	CALF
1980	15	1	*4*	*10*	4	10	1
1981	17	6	*4*	*8*	4	8	6
1982	24	8	*6*	*10*	6	10	8
1983	32	8	*10*	*14*	10	14	8
1984	41	9	*14*	*18*			9
1985	55	14	*18*	*23*			15
1986	70	15	*25*	*30*			16
1987	82	12	*32*	*38*			19
1988	98	16	*38*	*44*			
1989	112	14	*46*	*52*			
1990	138	26	*53*	*59*	38	75	23
1991	171	33	*66*	*72*	65	82	34
1992	185	14	*82*	*89*	79	90	33
1993	214	29	*89*	*96*	65	98	
1994	241	27	*103*	*111*	93	127	32
1995	280	39	*116*	*125*	73	157	19
1996	370	90	*135*	*145*	109	179	80
1997	465	95	*180*	*190*	170	218	77
1998	549	87	*227*	*238*	206	256	87

[a] numbers extrapolated from fall herd counts and prior year estimates,

[b] numbers observed during fall herd counts

[c] observations made by P.J.P. Gogan in 1980 to 1987,O.L. Wallis in 1990,1992,1993, L. George in 1994, S. Koening in 1995.

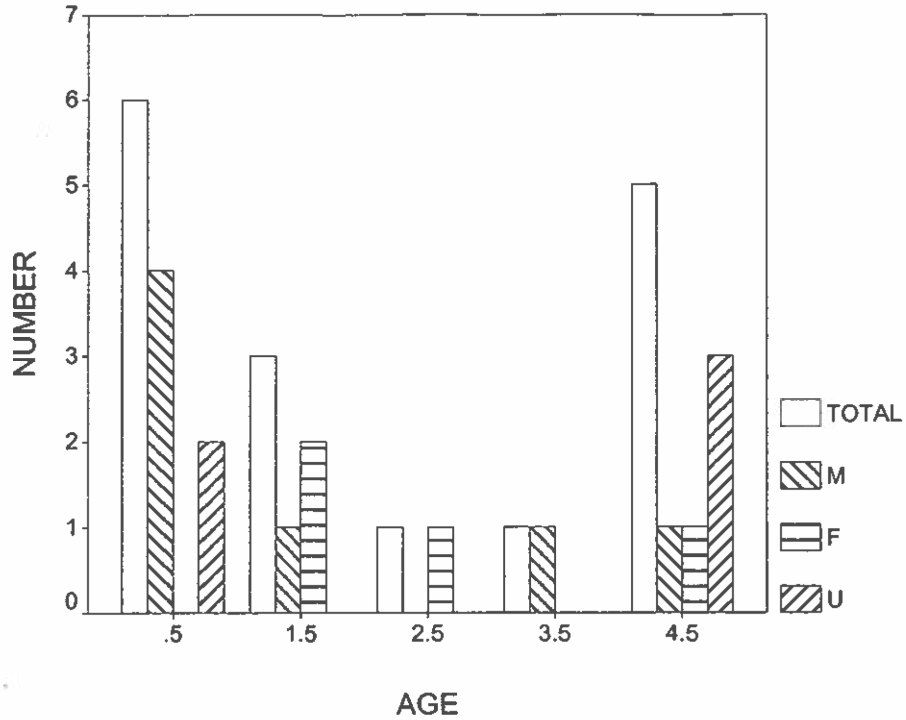

Figure 7. Age distribution of tule elk remains recovered between 1995 and 1998, Point Reyes National Seashore, California. (M = male, F = female, U = unknown sex)

Table 5. Diseases reported in seven elk recovered and necropcied, 1996 to 1998, Pt. Reyes National Seashore, Cal.

Disease	**Frequency (%)**
Blue tongue	28.6
Pneumonia	28.6
Bronchitis	28.6
Abomasitis	57.1
Enteritis	28.6
Colitis	14.3
Steatitis	14.3
Enterocolitis	28.6
Mycardutus	14.3
Encephalomalacia	28.6
Presumptive selenium deficiency	28.6
Umbilical infection	28.6
Intestinal cestodiasis	14.3
Pancreatic necrosis	14.3
Johne's disease	28.6

not. Several additional cow elk showed signs of scouring. One instrumented cow was removed in 1998 for this reason. These animals were repeatedly fecal-tested for Johne's disease, but the tests remained negative (S. Shideler personal communication). From necropsy reports prepared by the California Department of Fish and Game and the Veterinary Health Sciences Laboratory, UC Davis of 7 animals, we determined that 15 factors contributed to poor health or death (Table 5). Although mountain lion and bobcat were observed on the elk range, the most numerous predators were the coyotes, which we observed on a regular basis. We found no evidence of direct predation by felids, such as covered carcasses. We found 1 calf that had been clearly gnawed by a canid but were unable to determine whether it was predation or scavenging.

Cow survivorship.--During the course of the study we continued to see an old cow that was marked during the original releases or was a calf born through spring of 1981. In reviewing park records we observed that 4 marked cows were observed approximately 10 or more years after release or tagging as calves (O.L. Wallis 1990 field notes). The "old cow" was removed in 1998 because of scouring to be tested for Johne's disease and upon fecal culture testing was shown to be negative for the disease. Based on these data from released or tagged calf elk, we estimated survivorship and longevity for adult females to be high as 18 years (Fig. 8). Four cows, excluding the case of capture myopathy, of the 38 collared cows died during the 3-year study, mortality rate of 0.035 yr^{-1}. The annual mortality for 1996, 1997, and 1997 was 0.150, 0.000, and 0.058, respectively (mean = 0.069, $n = 3$, SE = 0.044). We plotted the 2 mortality rates derived above as linear constants resulting in an average longevity of approximately 17 years (Fig. 9).

Calf survivorship.--In 1996, 1 of 12 marked calves died by fall, survivorship was 0.92. In November 1996, we counted 380 elk of which 90 were calves. In spring and summer of 1997, we captured 26 calves of which 22 survived through the summer. Calf survivorship was 84.6%. Also in 1997, we estimated by direct count that 121 calves were born and counted 103 calves by late summer. Calf survivorship was 84.4%. A single instance of winter calf mortality was noted for 1997. Extrapolating from this observation, the winter calf survivorship was estimated at 0.96. This resulted in an overall survivorship estimate of 0.81 for 1997. In 1998, we captured 28 calves of which 24 (85.7%) survived to the fall herd count. Aged remains of tule elk showed a similar pattern of higher mortality among younger age classes (Fig. 7).

Density

We monitored the location, habitat use, and survivorship of the remaining 34 collared cow elk and 66-tagged calves through December 1998. We located instrumented cows at dawn, dusk, and night that indicated the elk did not use different habitats than those occupied during the day. The observations indicated that elk remained in the same areas at dawn that they occupied overnight. We observed movement within habitat types away from roads and trails as park visitors arrived in late morning. Movement towards roads and trails was often seen late in the day, but usually did not take the animals into different habitats. We noted that the elk segregated into two sub-herds, north and south. The larger group was located in the south (Fig 10). Based on an analysis

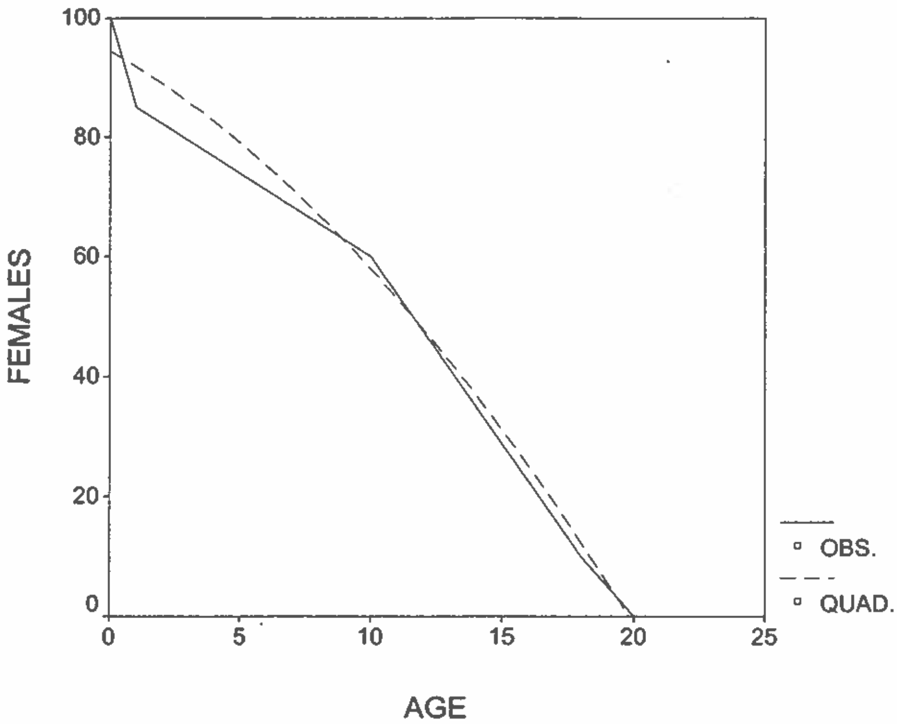

Figure 8. Survivorship curve for original tule elk cows released between 1978 and 1982, Point Reyes National Seashore, California.

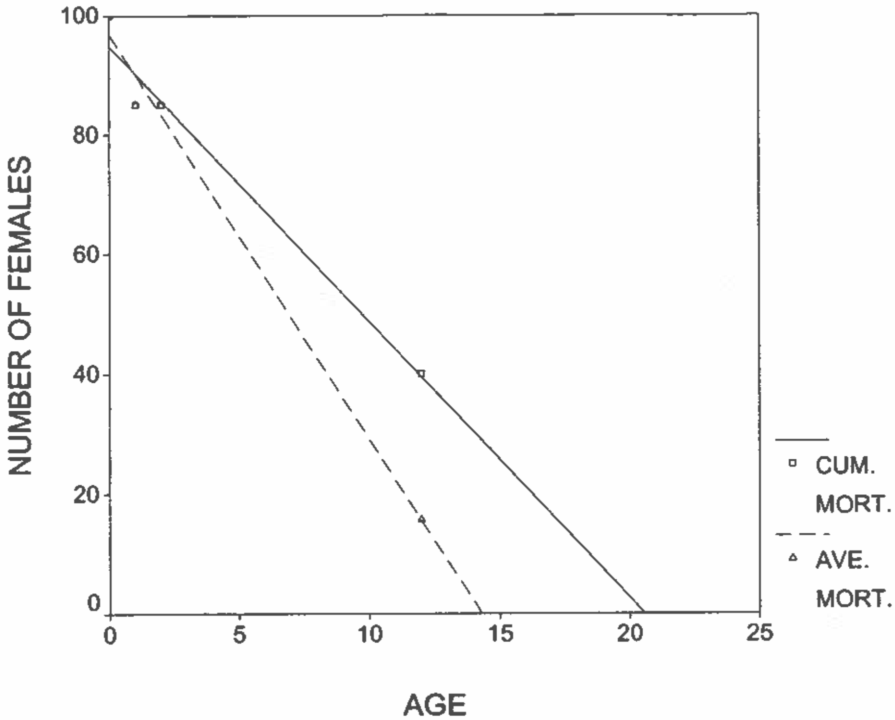

Figure 9. Survivorship curves for estimated for tule elk cows, 1995-1998, Point Reyes National Seashore, California.

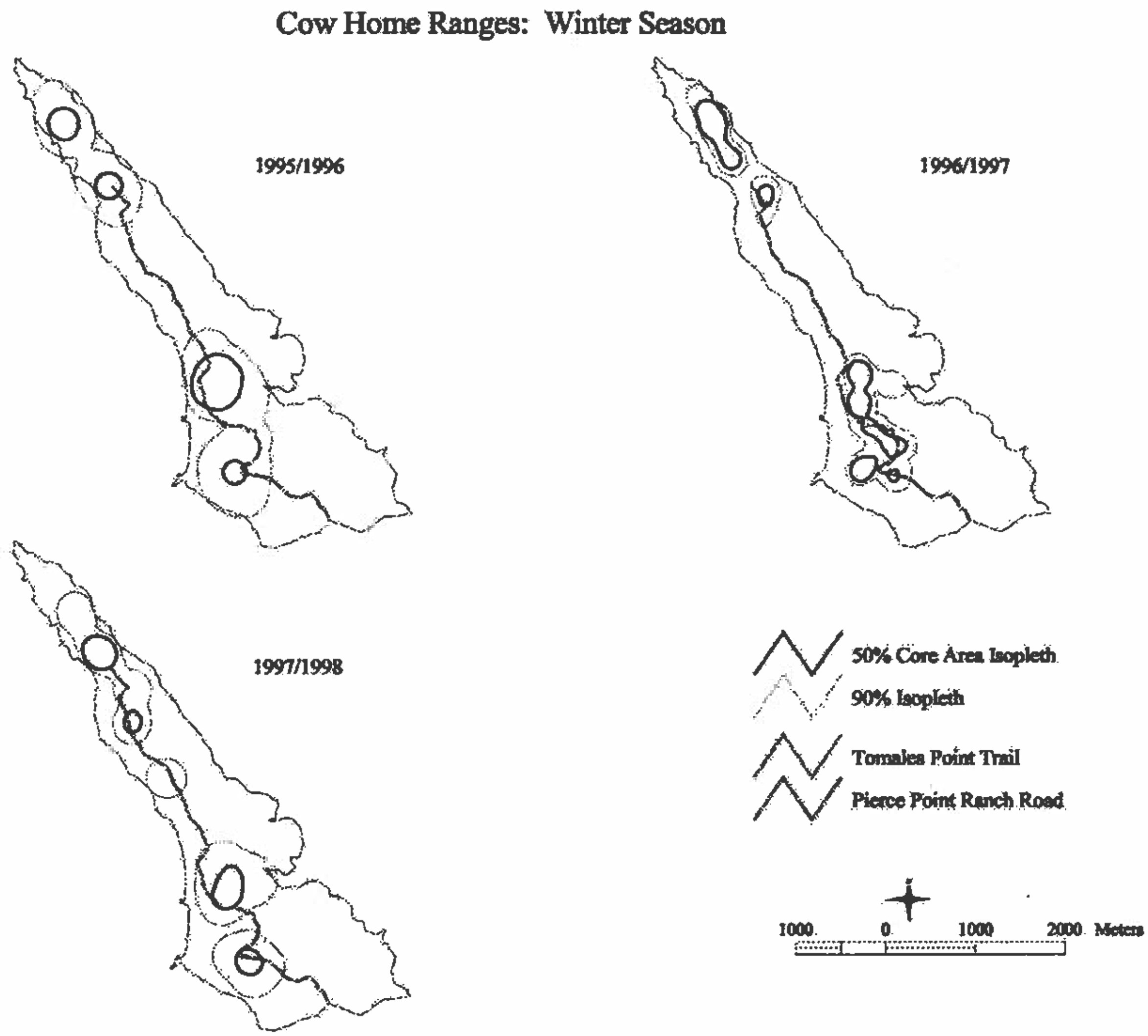

Figure 10A. Cow tule elk herd distribution during four biological seasons, (A) winter, (B) calving, (C) summer, and (D) rut, 1995-96, 1996-7, and 1997-8, Point Reyes National Seashore, California.

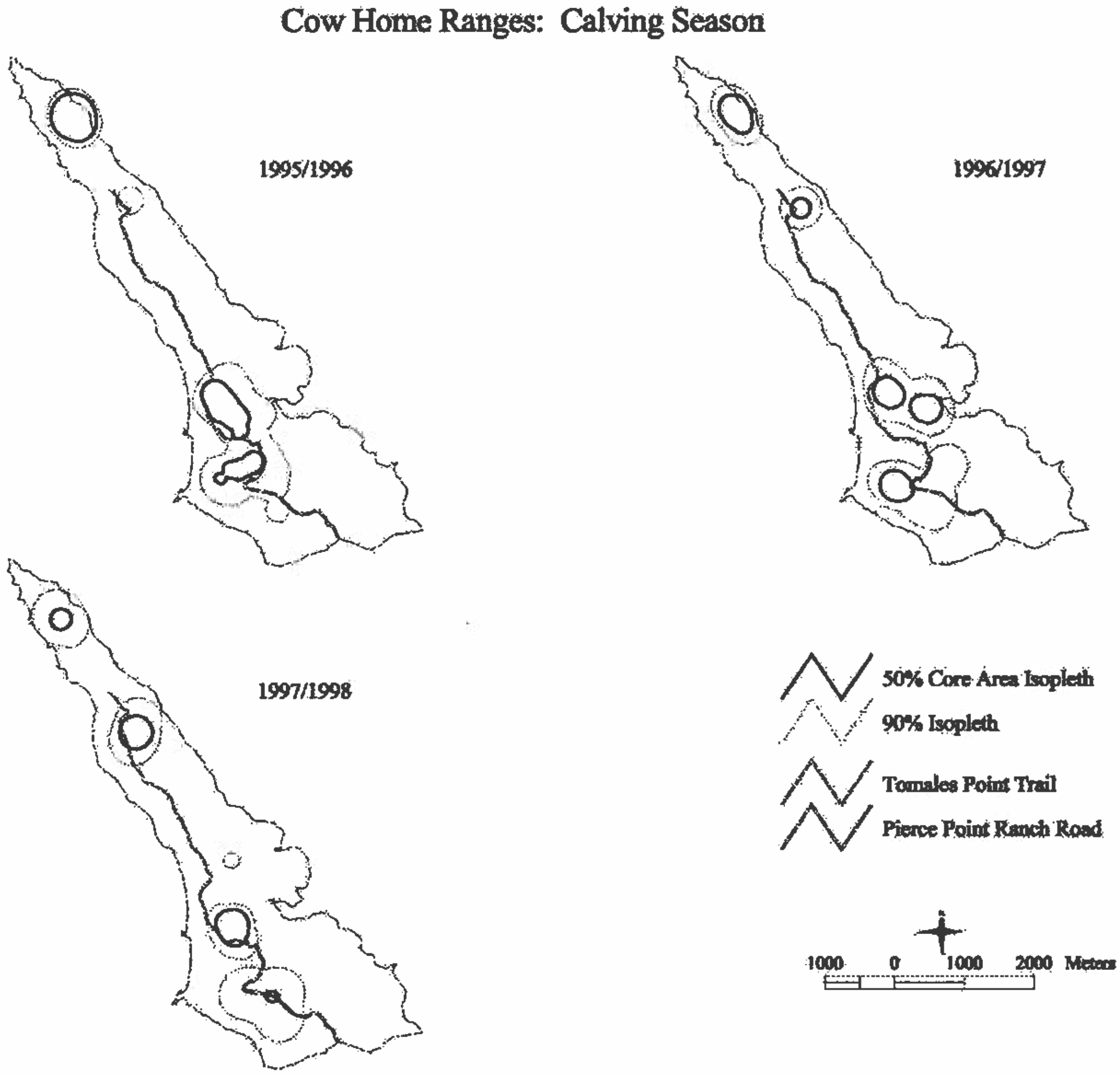

Figure 10B. Cow tule elk herd distribution during four biological seasons, (A) winter, (B) calving, (C) summer, and (D) rut, 1995-96, 1996-7, and 1997-8, Point Reyes National Seashore, California.

Cow Home Ranges: Summer Season

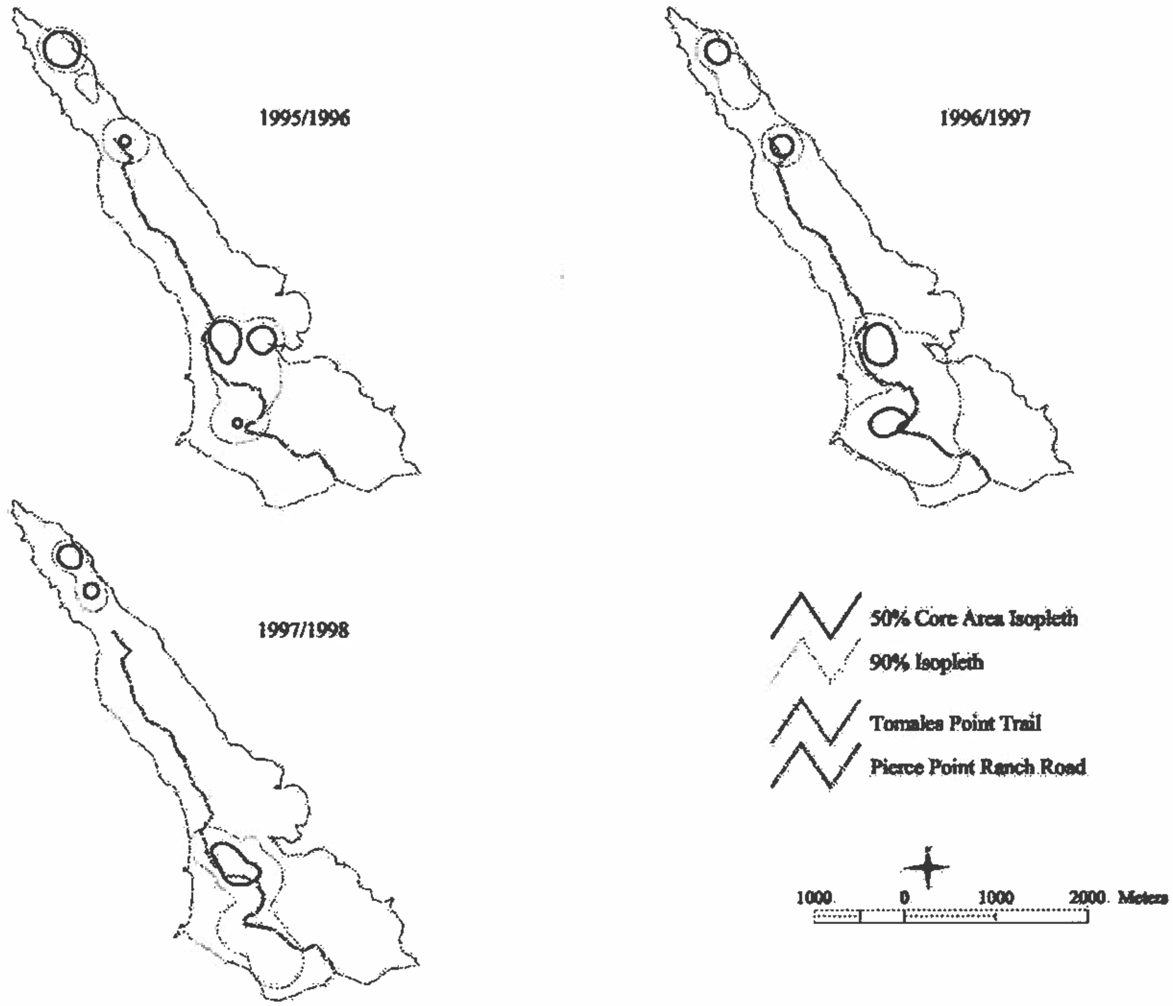

Figure 10C. Cow tule elk herd distribution during four biological seasons, (A) winter, (B) calving, (C) summer, and (D) rut, 1995-96, 1996-7, and 1997-8, Point Reyes National Seashore, California.

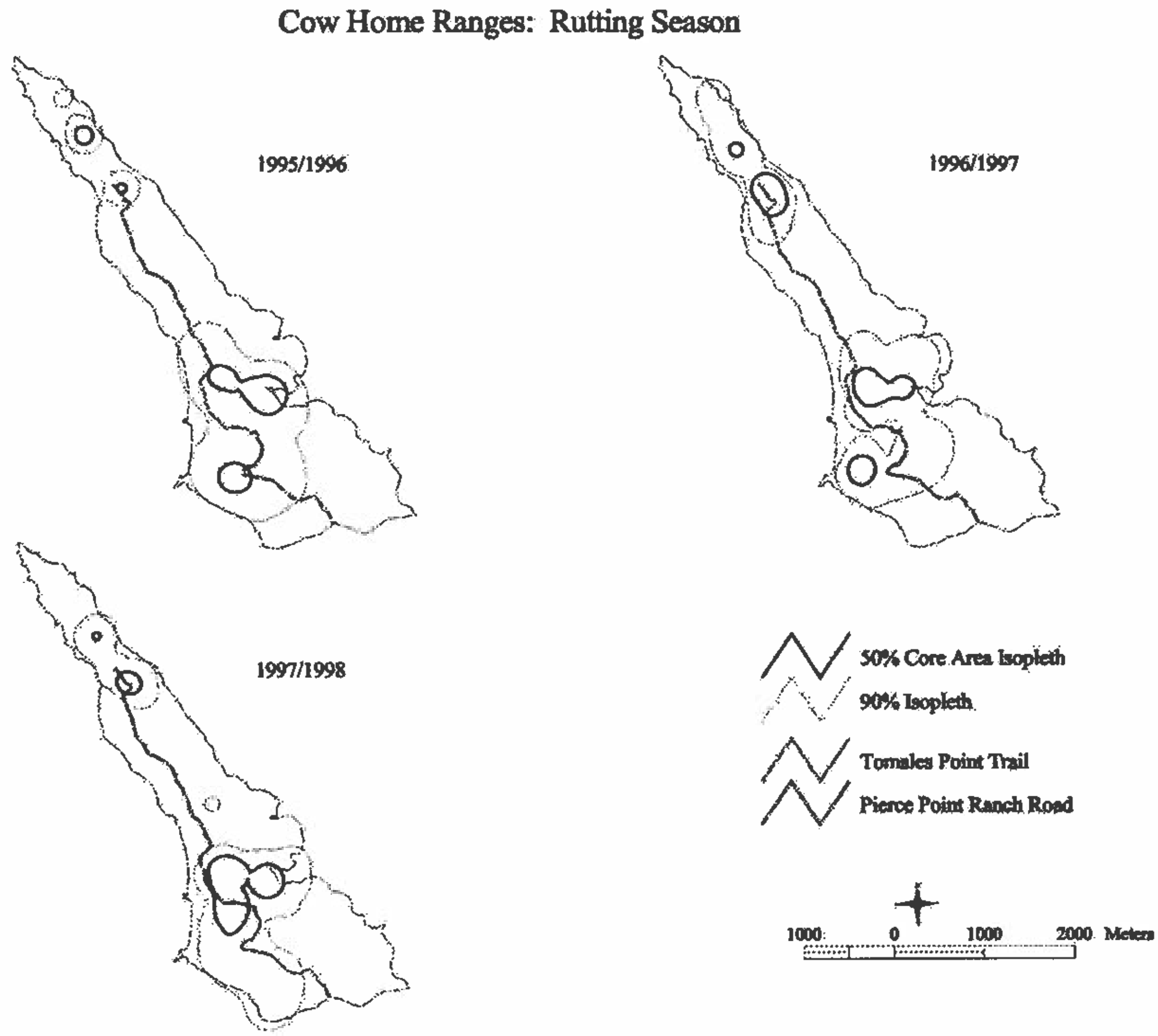

Figure 10D. Cow tule elk herd distribution during four biological seasons, (A) winter, (B) calving, (C) summer, and (D) rut, 1995-96, 1996-7, and 1997-8, Point Reyes National Seashore, California.

of relocations some cows occasionally had one relocation in the other group then returned to their original group. We observed an increase cow-calf herd size from 1996 to 1998 and observed no change in herd range size 354, 351, versus 328 ha (90% CI) (Table 6). Cow-calf densities were 0.733, 0.840, and 1.045 elk ha^{-1} in 1996, 1997, and 1998, respectively. Herd range sizes for the cow-calf sub-herds were different between the north and southern groups--94 versus 249 ha. Bull herd range was 609-ha and densities were 0.279 elk ha^{-1} in 1997 (Table 7). The core use areas of cow-calf sub-herds and bulls groups were highly displaced from each other (Fig. 11). Cow-calf herds were located in grassland and grassland-shrub habitats while bulls were located in heavy brush habitat. We applied the cow-bull density estimates to the entire range; we estimated maximum densities of 741 cows-calves and 282 bulls for the 1052-ha range. This translates to an estimated upper limit of 1023 elk during wet years, such as El Niño intervals, precipitation > 1024 mm $year^{-1}$.

Herd Growth Stabilization Modeling

We modeled the time necessary to reduce the net reproductive rate to one with three scenarios: removal, contraception, and removal/contraception combined (Greene, C. Personal Communication). Lambda was reduced to 1.059 after 7 years by removing 50 bulls and cows yr^{-1}. By adding contraception to this removal of bulls and cows λ was reduced to 1.052. Contraception of 50 of the cows reduced λ, but it remained above 1 (1.097) after 7 years. Lambda was reduced to 1.0 within 5 years by contraception of 50 cows and removing 50 cows (Fig. 12).

DISCUSSION

Demographically, the Point Reyes herd was at the upper limit of estimated values for population parameters and growth at the end of the study period. Adult survivorship was approximately 95%, similar to values reported by Eberhardt et al. (1996) for Rocky Mountain elk (*C. e. nelsoni*) in eastern Washington. Calf survivorship was 85%, which was higher than 60% reported for Owens Valley tule elk (McCullough 1969) and similar to that of domestic sheep (Caughley 1976:191). Cow longevity was also greater--approximately 17 years versus 10 years for the Owens valley (McCullough 1966). Allen (1996) reported an annual growth rate of 0.213 for Rocky Mountain elk in Bandelier National Monument, New Mexico similar to the Point Reyes mean of 0.223. McCullough (1969) estimated the maximum theoretical population growth rate for tule elk to be 0.25. Point Reyes elk herd had a growth rate of 0.194 based on the exponential model, which is 0.054 higher than the Owens Valley tule elk herd (McCullough 1969) but similar to 0.20 reported by Eberhardt et al. (1996). By calculating the population doubling time ($2N_o = N_o e^{rt}$) using the estimated exponential rate of increase (0.194) the Point Reyes herd was doubling every 3.6 years during the study period. Gogan and Barrett (1987) reported herd growth rates estimates to be r = 0.17 and r = 0.29 at Point Reyes. Both values were in the range of rates of increase observed in this study. They noted that the higher rate occurred from 1982 to 1984, period coinciding with the first El

Table 6. Density estimates for Tomales Point cow tule elk (*Cervus elaphus*) herds, Point Reyes National Seashore, California.

Seasonal cow elk home range size (90 % C.I.), northern and southern portions of the Tomales Point tule elk range, Point Reyes National Seashore (Nov. 1995 - Oct. 1996)

	Range Size (ha)		
Season	**North**	**South**	**Total**
Winter	169	267	436
Calving	65	198	263
Summer	82	172	254
Rut	53	408	461
Mean	92	261	353
S.E.	26.3	52.9	55.1

Seasonal cow elk home range size (90 % C.I.), northern and southern portions of the Tomales Point tule elk range, Point Reyes National Seashore (Nov. 1996 - Oct. 1997)

	Range Size (ha)		
Season	**North**	**South**	**Total**
Winter	85	144	229
Calving	74	212	286
Summer	91	318	409
Rut	147	333	480
Mean	99	251	351
S.E.	16.3	44.9	57.8

Seasonal cow elk home range size (90 % C.I.), northern and southern portions of the Tomales Point tule elk range, Point Reyes National Seashore (Nov. 1997 - Oct. 1998)

	Range Size (ha)		
Season	**North**	**South**	**Total**
Winter	125	220	345
Calving	110	150	260
Summer	43	204	247
Rut	94	366	460
Mean	93.3	235	328
S.E.	17.8	46.2	49.1

Table 7. Density estimates for Tomales Point bull tule elk (*Cervus elaphus*) herds, Point Reyes National Seashore, California.

Bull elk home range size (90 % C.I.), northern and southern portions of the Tomales Point tule elk range, Point Reyes National Seashore (1997)			
	Range Size (ha)		
	Total	**Non-breeding**	**Rutting (mid July - mid Oct.)**
All Bulls	609	799	740
Prime Bulls	660	655	909

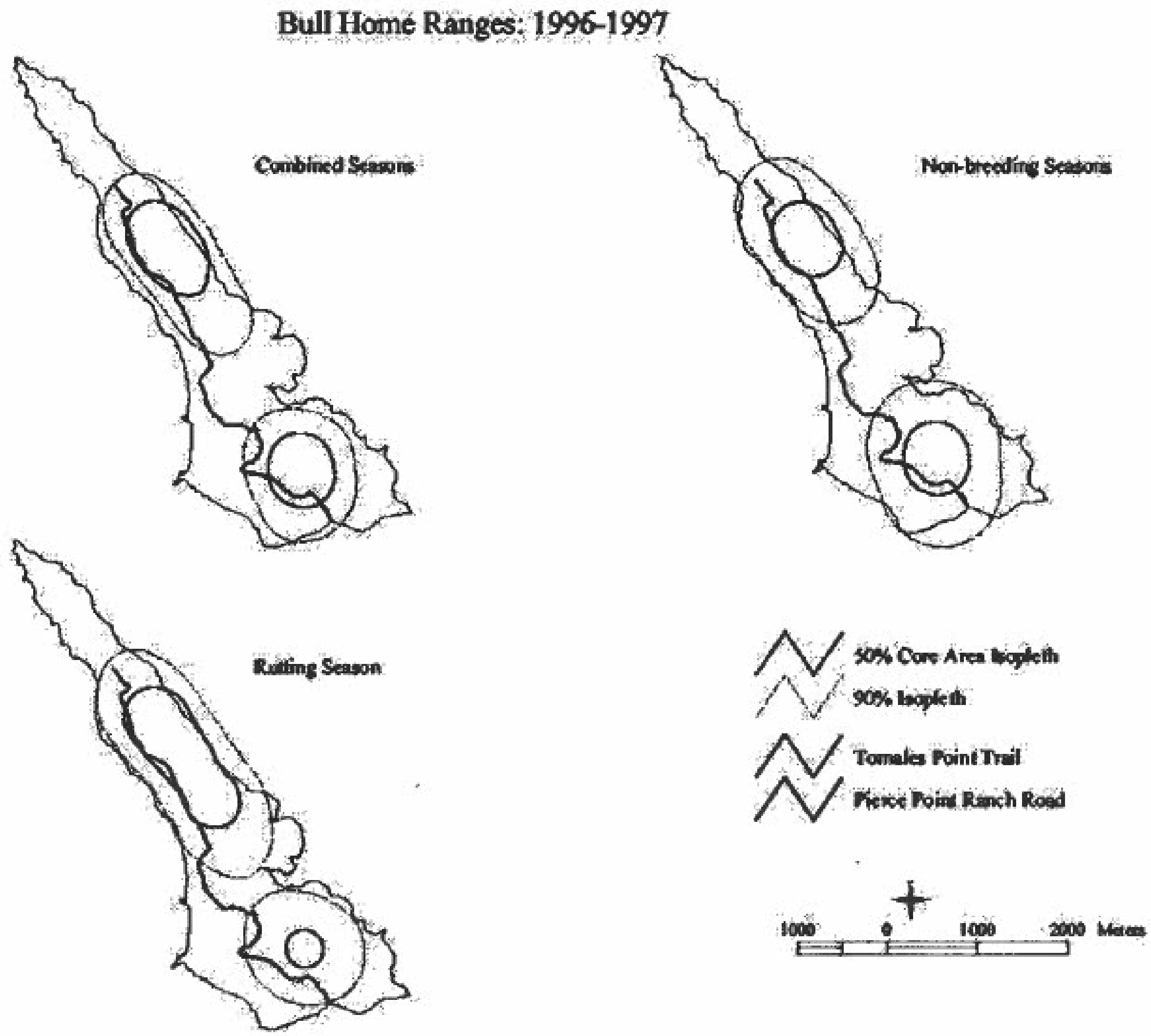

Figure 11. Bull tule elk herd distribution for 1996-1997, Point Reyes National Seashore, California.

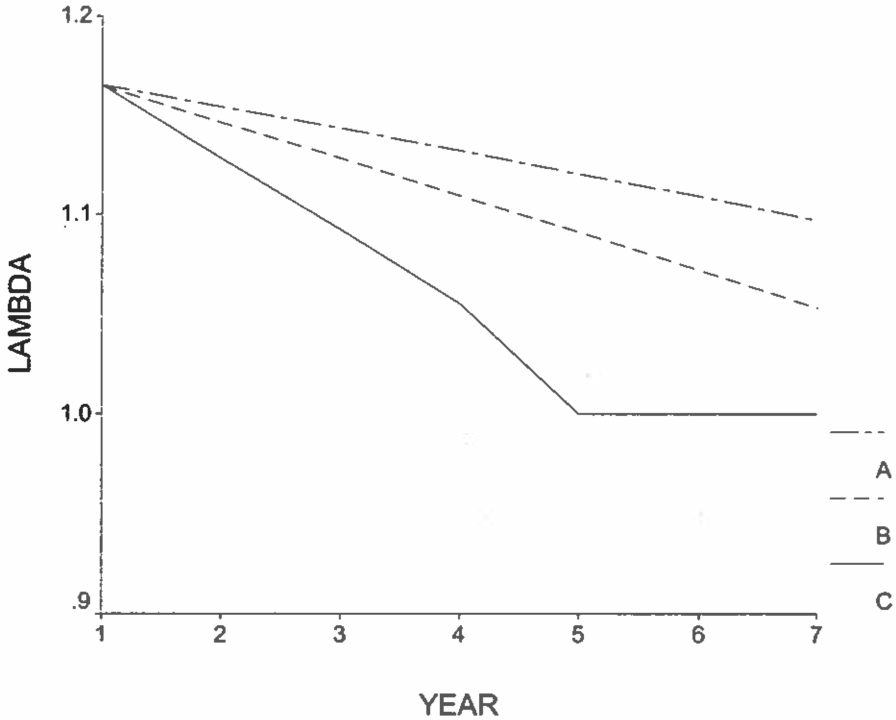

Figure 12. Population rate of increase (λ) over time for three population reduction scenarios; (A) contraception of 50 cows only, (B) contraception of 50 of the cows and removal of 50 cows and bulls (C) contraception of 50 of the cows and removal of 50 cows.

Niño event. This early period is confounded by the fact that the elk population was small, cattle were removed from the range, and vegetation was released from intensive grazing pressure.

By combining Gogan and Barrett's (1987) strong El Niño observations and ours, there is significant increase in growth rate of the population during these events. During the herd growth period between El Niño precipitation events 1982 to 1994, we found evidence of declining r with increasing N supporting the idea that density related growth rates may well be occurring during dry years. However, higher than normal precipitation during the El Niño years of 1995 through 1997 resulted in higher forage and calf production overriding density effects that appeared before 1995. In 1982, cattle were removed from the range, releasing the vegetation from grazing pressure while the tule elk herd was still small, thereby confounding the precipitation results. McCullough (1992) described a theoretical density-dependent reproductive response for bighorn sheep as a flat curve until the curve sharply dropped at the high population density. Negative population response occurred quickly at a critical high density. Hassell's (1975) empirical study supported this pattern. The Tomales Point herd appeared to be in that flat or no response phase during the study period. When central California coast experiences several years of drought, we predict the final growth phase described by McCullough (1992), i.e. decreasing growth, zero growth, and a sharp decline.

During simultaneous counts using aerial, ground-drive, and horseback counts, we think that ground counts underestimated the number of calves and aerial counts underestimated the number of spike bulls. Both methods resulted in higher estimates of cows. Ground-drive count bias was most likely due to difficultly differentiating older calves from cows. This would be likely with student observers. Aerial count bias was likely due to the greater distance between observer and elk than that of ground-drive and horseback counts. We think that horseback counts provide better herd composition estimates because observers approach elk more closely while riding permits the observer to cover the range from a higher vantage point, increasing visibility, and traversing the range more efficiently, minimizing the potential for double counting. Therefore, the horseback counts provided a reliable means of obtaining data on observed numbers of cows, calves, spikes, and bulls.

Though coyote sightings were more common in 1997 than in previous years, no instance of predation on neonates was documented. We observed a calf carcass with evidence of coyote feeding but the cause of death was indeterminate. Some of the calves that died emitted an odor of rotting flesh and we observed puss around the umbilicus. Two calf carcasses that were later necropsied had bacterial infections. There was one instance of winter calf mortality noted for 1997. A particularly small marked individual disappeared in December. The last time it was seen it was noted as having its hindquarters heavily covered with feces. This led to some speculation that this calf was putatively afflicted with Johne's disease. However, several scouring cow elk were seen at that time, 2 of them were collared individuals that had repeatedly tested negative for Johne's disease. Diarrhea probably is not a positive indication of Johne's disease. Fecal culture should be used to confirm clinical pathology prior to management decisions regarding the disposition of afflicted animals. Given the fact that we observed a number of newborn calves with umbilicus infections, we think bacterial infection may be an important source of neonatal mortality.

In 1997 park management began an experimental contraception program to assess its feasibility for regulating the Point Reyes herd. Contraception temporarily blocks pregnancy, thereby eliminating the possibility of natural selection to operate on life history stages of individuals. Kucera (1991) and McCullough (personal communication) report that tule elk exhibited much less genetic variation than conspecifics because of a series of extremely low population numbers experienced since their near extinction. However, deleterious effects of reduced genetic variation on tule elk have yet to be demonstrated. Without the potential to increase genetic variation through mutation and recombination, the Point Reyes herd could eventually suffer from problems associated with inbreeding depression or genetic drift to extinction (Allendorf 1983, Chesser 1983).

The genetic consequences of contraception remain to be explored for the Tomales Point herd. Natural selection operates on individuals in a population because of genetic differences among them (Alcock, J. personal communication) and unmanaged contraception could prevent individuals from entering the population limiting the palette of genetic diversity.

Park management and California Department of Fish and Game set a goal to limit the population to 600 elk on the range. It was estimated that this number, if held, should ameliorate the range impacts of the elk as forage production drops during dry years (Bayless 1998). If KCC of the range drops below 600 due to poor range production, we would expect some density-dependent effects to appear such as increased mortality from disease, reduced calving rates, lower cow:calf ratios and greater bull mortality.

The exponential growth model of the Tomales Point herd indicates that the current population growth phase shows little evidence of density dependence or natural regulation during our study. Quality and quantity of forage appear to remain high and the elk appear to be in good condition. Will micronutrients become a limiting factor on the elk range? Micronutrients (Se, Cu) deficiencies can translate into poor health condition including increased clinical expression of Johne's disease (Gogan 1986).

Using a simple model we examined the effort required to reduce the net reproductive rate from > 1.0 to 1.0. From the model results a combination of removal and contraception would have the most rapid reduction of net reproduction rate. We think the model reflects the order of magnitude of effort required to bring the population at Tomales Point to relative equilibrium.

At Tomales Point changes in population growth rate was associated with precipitation and may be increased during strong El Niño years. During these periods of good plant production we estimate the KCC of the range to be about 1000 animals based on our density estimates and extrapolation of declining growth rates with population size during inter-El Niño periods. California experiences prolonged periods of drought that will significantly lower KCC of the range. In a closed system like Tomales Point with no emigration, we would expect the herd to overshoot KCC and die back during prolonged drought.

In conclusion our KCC estimates are based on density determinations for cows and bulls that tended to utilize different parts of the Tomales Point range. Our estimate of 1000 elk does not account for differences in forage quantity or quality. We would expect that during drought years KCC would be much reduced, as much as 50% or more. Based on population growth rates and population size for dry years KCC would be about 350 animals. Although Tomales Point has three species of predators, predation was of little consequence in elk mortality during this study. Disease played a role in the mortalities we observed. Given the population growth characteristics this population can rebound quickly. Removal rates should be optimized using current demographic information to effectively reduce the population rate increase and remain cost effective for management.

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